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A REVIEW OF THE BATS OF THE ENDEMIC WEST
INDIAN GENUS *EROPHYLLA*

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The subfamily Phyllonycterinae of the family Phyllostomatidae is comprised of the genera *Brachyphylla*, *Phyllonycteris*, and *Erophylla*; all are endemic to the West Indies. Two species are presently included in the genus *Erophylla*: *E. bombifrons*, which occurs east of the Windward Passage on Hispaniola and Puerto Rico and *E. sezekorni*, which is found on most of the major islands west and north of the Windward Passage including Cuba, Jamaica, and the Bahamas. The present taxonomic status of populations of *Erophylla* rests in large measure upon studies involving relatively few specimens from limited geographic areas. No attempt has yet been made to determine and evaluate variation within the genus as a whole.

In the process of reevaluating the taxonomic status of all named populations within this genus, I have examined 624 specimens. Names used throughout the greater part of the text are those in current use. Nomenclatural changes that I propose are given at the end of the discussion.

TAXONOMIC HISTORY

Gundlach (1861) erected the genus *Phyllonycteris* for two new species of bats from Cuba (*poeyi* and *sezekorni*). Miller (1899) described *Phyllonycteris bombifrons* of Puerto Rico and *P. planifrons* of the Bahamas. Elliot (1905) described *Phyllonycteris santa-cristobalensis* of Hispaniola. Subsequently, Miller (1906) erected the genus *Erophylla* to include

(as separate species) *sezekorni*, *bombifrons*, *planifrons*, and *santacristobalensis*.

Allen (1917) proposed a taxonomic arrangement for this group that is basically the one most in use at present. Allen treated *santacristobalensis* as a subspecies of *Erophylla bombifrons* and applied the name *Erophylla sezekorni* to populations in Cuba, Jamaica, and the Bahamas. He proposed the name *E. sezekorni syops* for the Jamaican population and treated *E. planifrons* Miller of the Bahamas as a subspecies of *E. sezekorni*.

Shamel (1931) treated *planifrons* as a distinct species when he described *E. planifrons mariguanensis* of the southern Bahamas. Koopman, et al. (1957) reported several new Bahamian records of *Erophylla* and adopted G. M. Allen's interpretations in treating *planifrons* as a subspecies of *E. sezekorni*. The interpretations of Allen also form the basis for the taxonomic treatment of the genus presented in Hall and Kelson (1959, pp. 147-148).

Recent studies of *Erophylla* have not dealt with intrageneric relationships. Silva Taboada and Pine (1969) discussed morphological and ecological features in the genus, but their comparisons were largely intergeneric. Baker and Lopez (1970) reported on the karyotype of *E. bombifrons* from Puerto Rico, but karyotypes from other populations of *Erophylla* are not available for comparison. Varona (1974) treated *Erophylla* as a subgenus of *Phyllonycteris* but retained the same species and subspecies names for populations as given in Hall and Kelson (1959).

According to Hall and Kelson (1959) there are two subspecies of *E. bombifrons*—the nominate race on Puerto Rico and *santacristobalensis* on Hispaniola. These authors recognize four subspecies of *E. sezekorni*—the nominate race on Cuba, *syops* on Jamaica, *planifrons* throughout most of the Bahamas (except for the extreme southern region) and *mariguanensis* in the southern Bahamas. Varona (1974) includes the Isle of Pines in the range of nominate *sezekorni* and records an unassigned subspecies of *E. sezekorni* from Grand Cayman in The Cayman Islands.

Several islands not indicated in previous accounts may now

be added to the list of islands whence *E. sezekorni* has been taken. Among these are Andros, Acklins, San Salvador, and Great Inagua, all of which are part of the Bahamas proper. Also included are Providenciales, North Caicos and Middle Caicos of the Caicos Islands (geographically a part of the southern Bahamas) and Cayman Brac in the Cayman Islands.

HABITS AND HABITAT

E. sezekorni is a relatively common bat in caves throughout the southern Bahamas. Walker, et al. (1975) states that members of this genus generally roost in the deeper and darker parts of caves. I found *E. sezekorni* on exposed surfaces and deep within solution cavities on the ceilings of caves, often in areas where much daylight penetrated. I usually saw members of this species in groups of four to 30 individuals. Two cylindrical solution cavities, each about 5 m deep, and 1 to 2 m in diameter, in the ceiling of a cave at Conch Bar, Middle Caicos, each contained about 50 individuals of *Erophylla* on 12 January 1972. Pale bats seen frequenting the blossoms of sisal (*Agave sisilana*) on North Caicos at dawn and dusk during February 1972 were identified by sight as this species.

Some of the individuals that I encountered in caves were extremely wary and flew away immediately upon being approached; others showed little concern even when a strong beam of light was focused upon them. Most often, however, individuals responded to a flashlight beam by moving their heads about rather nervously, then flying off to another part of the cave.

Most of my observations were made during the day when the bats were hanging from the walls and ceilings of caves and were relatively inactive. However, on 30 January 1972, when I visited the cave at Conch Bar, Middle Caicos, about one hour before sunrise, I found many *E. sezekorni* flying inside the main chamber. Several individuals were seen landing on a particular stalactite and on a lateral projection on the cave wall that had water slowly flowing over the surfaces. The bats did not hang by their feet in the conventional manner after landing at these sites but lit in an upright position, grasping the rock surface with all four appendages; the

wings were folded against the body. The bats maintained this position for only 2 to 5 seconds at a time and four or five individuals appeared to make a number of return trips at less than 1-minute intervals. That the bats were drinking water seems a likely possibility, although I did not directly observe them doing so. None of the dry surfaces was visited by bats in this fashion.

FETAL DEVELOPMENT

Data from 91 gravid or lactating females and immature individuals indicate that most prenatal development takes place during the first part of the year and that parturition probably occurs most often in early summer. Females bearing small embryos have been taken during early and late February and individuals with well developed fetuses have been obtained in April and May. Lactating females have been collected in June and many immature (probably newborn) individuals have been taken in July. Immature individuals approaching adult size may be found during August. Further details on nursing females and developing young are presented in Table 1.

MORPHOLOGICAL COMPARISONS

Coloration: Specimens of *Erophylla* show much variation in coat color and for the most part I detected no consistent differences among presently recognized subspecies. Individuals of *E. b. santacristobalensis* (Hispaniola) are more reddish tan than the drab, darker brown specimens of *E. b. bombifrons* (Puerto Rico) but specimens of the four subspecies of *E. sezekorni* range from pale buff to medium or dark brown and many individuals have white on the head.

Part of the range of variation and overlap in color among samples from different islands is shown in Fig. 1. Specimens included in these comparisons are those that I recently collected on Crooked Island, Mayaguana and the Caicos Bank, and specimens from the Schwartz collection that were prepared between 1961 and 1968 and kept under similar storage conditions. Comparisons were made with a Gardner Color and Color-Difference Meter (Model XL-10). This instru-

TABLE 1. Seasonal data on nursing females and developing young in the genus *Erophylla*.

Date Collected	No. and Condition of Specimens Examined	Locality
11 February (1928)	1 small embryo	Hispaniola
26-28 February (1917)	11 small embryos	Cuba
10 April (1972)	2 fetuses (crown-rump length = 10.6 and 11.1 mm, \bar{x} = 10.9)	Crooked I. (Bahamas)
27-28 April (1968)	9 fetuses (crown-rump length = 14.0-17.5 mm, \bar{x} = 15.8)	Andros I. (Bahamas)
5 May (1972)	6 fetuses (crown-rump length = 13.7-20.3 mm, \bar{x} = 17.9)	Crooked I. (Bahamas)
13 June (1966)	3 lactating females	New Providence (Bahamas)
26 June (1966)	1 lactating female	San Salvador (Bahamas)
5-6 July (1916)	2 immature individuals and 1 nursing female	Puerto Rico
9 July (1935)	41 immature individuals	Cat I. (Bahamas)
22 July (1904)	5 immature individuals	Great Abaco (Bahamas)
27 July (1938)	8 immature individuals (total length = 55-64 mm, \bar{x} = 59.9)	Great Inagua (Bahamas)
20 August (1910)	1 immature individual near adult size	Jamaica

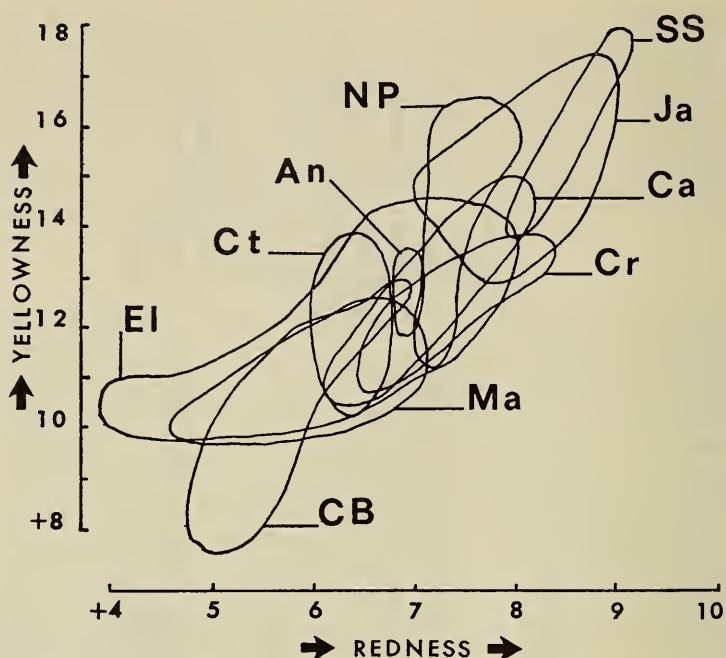


FIG. 1. Color variation in 10 samples of *Erophylla sezekorni* as follows: El, Eleuthera; Ct, Cat Island; An, Andros Island; NP, New Providence; SS, San Salvador; Ja, Jamaica; Ca, Caicos Islands; Cr, Crooked Island; MA, Mayaguana; CB, Cayman Brac. Lines circumscribe values obtained with a Gardner Color and Color-Difference Meter.

ment measures color reflected from a flat surface on three scales. The L scale indicates paleness and ranges from 0 (black) to 100 (white). The a scale indicates redness when the reading is positive and greenness when negative, whereas the b scale measures yellowness when the reading is positive and blueness when negative. A reading of L 50, a 0, and b 0 indicates gray. Readings were taken on the posterodorsal surface of the skins covering an area 20.0 mm in diameter. The instrument scales were calibrated on a white standard according to values assigned to the standard by the manufacturer (L 91.6, a -1.3, b -0.1).

A considerable amount of variation in color occurs within

samples from the same locality. Some may be attributed to ontogenetic changes, molt condition, atmospheric bleaching (although the caves that I visited in the southern Bahamas were well aerated and had no strong smell of ammonia) or to fading of specimens in storage. However, segregating available material according to age, season, and storage history would result in many exceedingly small samples for comparison. I do not believe that color differences can be used effectively to distinguish subspecies of *Erophylla* as they are currently defined, but more detailed color evaluations will require additional material of comparable status.

Mensuration: Measurements, and the manner in which they were taken for this study, are as follows: skull length (distance between posteriormost portion of skull and tips of incisors), condylobasilar length (distance from posterior margin of condyles to a line connecting posterior margins of alveoli of anteriormost incisors), maxillary toothrow (distance from posterior margin of third molar to anterior surface of corresponding canine at its base), breadth at canines (distance across snout at level of canines, including outer tooth surface), postorbital breadth (least distance across skull, at a point posterior to orbits), zygomatic breadth (greatest distance across zygomata), breadth of braincase (greatest width of braincase), cranial height (greatest vertical distance between top of skull and ventralmost point of occipital bone), breadth at canines/breadth of braincase (a percentage), breadth of braincase/skull length (a percentage), cranial height/skull length (a percentage), total length (measurements taken on fluid-preserved specimens are combined with measurements taken from labels on study skins), forearm length including carpal elements (measurements taken on fluid-preserved specimens and study skins are combined), ear length (from notch; taken only on fluid-preserved specimens), tail length (from fluid-preserved specimens only), tibia length (from fluid-preserved specimens only).

Mensural comparisons include specimens from 17 localities shown in Fig. 2. Statistical data for selected measurements are presented in Table 2. A test for statistically significant differences using a one way classification analysis of vari-



FIG. 2. Map of the Bahamas and Greater Antilles showing localities for 17 samples of *Erophylla* as follows: GA, Great Abaco; NP, New Providence; An, Andros; El, Eleuthera; Ct, Cat Island; Ex, the Exumas; Lg, Long Island; SS, San Salvador; C-A, Crooked Island and Acklins Islands; MA, Mayaguana; CA, Caicos Islands; GI, Great Inagua; Cu, Cuba; CB Cayman Brac; Ja, Jamaica; Hi, Hispaniola; PR, Puerto Rico. WP=Windward Passage.

ance was conducted. Specific comparisons for selected samples representing different subspecies pairs were made. The results of this test are summarized in Table 3. All measurements are in millimeters and sexes have been combined in these comparisons.

There are no obvious well-marked differences in comparisons between and among any of the subspecies, although statistically significant differences are apparent in each subspecies for at least two (*E. bombifrons santacristobalensis* with *E. b. bombifrons*) to as many as six *E. sezekorni planifrons* with *E. s. mariguanensis*) of the 15 characters examined. One character (forearm length) shows statistically significant differences in all comparisons, yet the range for this character for 508 individuals (from six named populations) is 41.6–50.0. Comparisons between selected samples of fluid preserved specimens and dried skins showed no significant differences in forearm length and I have combined wet and dry measurements in all comparisons.

Furthermore, there may be more variation within the limits

TABLE 2. Selected measurements from six samples of *Erophylla*; each island includes the type-locality for one of the six nominal subspecies. Each set of numbers includes mean and sample size (row 1), range (row 2), and standard deviation and coefficient of variation (row 3).

	New Providence <i>planifrons</i>	Mayaguana (<i>mayaguanensis</i>)	Cuba (<i>sezekorni</i>)	Jamaica (<i>syops</i>)	Hispaniola (<i>santacristobalensis</i>)	Puerto Rico (<i>bombifrons</i>)
Length	24.5 - (18)	25.2 (6)	24.3 (31)	24.7 (29)	24.1 (18)	24.3 (18)
Skull	23.7 - 25.4	24.6 - 26.1	23.6 - 25.1	23.7 - 25.7	23.4 - 25.0	23.3 - 24.9
	0.52 2.12	0.54 2.16	0.38 1.58	0.49 2.00	0.44 1.84	0.44 1.79
Cranial	8.4 (19)	8.5 (6)	8.3 (44)	8.4 (29)	9.0 (21)	9.1 (18)
Height	8.1 - 8.8	8.3 - 8.8	7.9 - 8.8	8.0 - 8.9	8.4 - 9.6	8.6 - 9.6
	— —	0.23 2.72	0.19 2.30	0.25 2.93	0.31 3.45	0.26 2.85
Forearm	46.0 (50)	46.6 (35)	45.4 (88)	46.5 (66)	46.7 (49)	47.7 (47)
Length	43.2 - 47.6	44.5 - 49.2	41.6 - 48.2	44.7 - 49.3	45.1 - 48.9	45.7 - 50.0
	0.99 2.16	0.96 2.06	1.29 2.83	1.07 2.31	0.97 2.08	0.94 1.98
Ear	19.7 (33)	19.8 (29)	19.3 (41)	19.3 (43)	16.9 (39)	17.3 (30)
Length	19.0 - 21.0	19.0 - 21.0	18.0 - 20.0	17.0 - 21.0	15.0 - 18.0	15.0 - 19.0
	0.59 2.97	0.58 2.92	0.79 4.08	0.85 4.40	0.83 4.94	0.84 4.84

TABLE 3. Results of F-test comparisons of four pairs of samples of nominal *Erophylla* for 15 character states; * indicates ($P < .05$), ** indicates ($P < .01$) ns indicates no statistical differences at the .05 or .01 levels of significance.

	Hispaniola vs. Puerto Rico (<i>santacristobalensis</i> vs. <i>bombifrons</i>)	New Providence vs. Mayaguana + Cacos Ids. (<i>planifrons</i> vs. <i>mariguaniensis</i>)	New Providence vs. Cuba (<i>planifrons</i> vs. <i>sezekorni</i>)	Cuba vs. Jamaica (<i>sezekorni</i> vs. <i>syops</i>)
Skull Length	ns	**	ns	*
Condylbasilar Length	ns	**	ns	*
Maxillary Toothrow	ns	ns	**	ns
Breadth at Canines	ns	ns	ns	ns
Postorbital Breadth	ns	ns	**	ns
Zygomatic Breadth	ns	ns	ns	ns
Breadth of Braincase	ns	*	**	ns
Cranial Height	ns	ns	ns	ns
Breadth at Canines $\times 100$	ns	**	ns	ns
Breadth of Braincase $\times 100$	ns	**	**	ns
Skull Length	ns	ns	ns	ns
Total Length	**	*	*	**
Forearm Length	ns	ns	ns	ns
Ear Length	ns	ns	ns	ns
Tail Length	ns	ns	ns	ns
Tibia Length	**	ns	ns	**

of any presently recognized subspecies in the genus than between subspecies. The greatest number of characters showing statistically significant differences (six) was found in the comparisons between *E. sezekorni planifrons* and *E. s. mariguanensis*. All specimens of *E. s. planifrons* in this particular series of comparisons are from New Providence (the type-locality). In at least three of these six characters there is actually a greater difference between the mean of the New Providence sample and that of some other sample within the range of *E. s. planifrons* than between the mean of New Providence material and that of the sample *E. s. mariguanensis*.

Also, examination of this material indicates that many of the mensural differences mentioned in the original descriptions of the various named taxa of *Erophylla* do not hold true, or at least are of a lesser magnitude than previously indicated.

Miller (1899) stated that *planifrons* differs from *sezekorni* in possession of very slender but complete zygomatic arches, a slightly broader and flatter rostrum, and a relatively smaller braincase. Actually the presence of complete zygomatic arches is characteristic of all members of the genus *Erophylla* and is one feature used to distinguish this genus from *Phyllonycteris*, all members of which have incomplete zygomatic arches. Also, I found no statistically significant differences (at the .01 or .05 levels) for the measurement breadth at canines, or for the ratio breadth at canines/breadth of braincase, but I did find a significant difference ($P < .01$) in the breadth of braincase/skull length ratio in the *planifrons* vs. *sezekorni* comparison. Eighteen specimens of *planifrons* ranged from 39.6 to 42.9 ($\bar{x} = 40.8$) whereas 31 specimens of *E. s. sezekorni* ranged from 37.7 to 41.6 ($\bar{x} = 40.0$) for this character.

Allen (1917) stated that *E. s. syops* of Jamaica differed conspicuously from *planifrons* and *sezekorni* in its "wider rostrum with molar rows nearly parallel instead of converging anteriorly." My comparisons between *syops* and *sezekorni* indicate no significant difference (at the .01 or .05 levels) for the measurements breadth at canines and breadth of braincase or for the ratio breadth at canines/breadth of braincase.

Shamel (1931) indicated that *E. p. mariguanensis* differed

mentally from *E. p. planifrons* in its larger size and smaller teeth but longer maxillary tooththrow. My comparisons between these two forms showed no statistically significant differences (at .01 or .05 levels) in total length or maxillary tooththrow but did ($P < .01$) for skull length. Eighteen specimens of topotypic *planifrons* ranged from 23.7 to 25.4 ($\bar{x} = 24.5$) for skull length whereas 27 specimens of *mariguanensis* from Mayaguana and the Caicos Bank ranged from 24.2 to 26.1 ($\bar{x} = 25.2$) for this character.

DISCUSSION

I believe that the designation of subspecies on the basis of the color and mensural differences discussed above is an over-refinement. Such an approach, in this case, if strictly and consistently applied, would result in further fragmentation of the *Erophylla* complex into additional weakly defined nomenclatural units. Differences between many of the currently recognized taxa are slight and much overlap occurs in most characteristics. I see no advantage in recognizing (or constructing) a host of subspecies within the genus *Erophylla*.

There are, however, two groups in this complex that are morphologically distinct (although some overlap occurs in all comparisons) and geographically separated. One group occurs west and north of the Windward Passage (Fig. 2), has a relatively long skull with low cranial profile, relatively long ears, and ranges in color from yellowish brown to dark brown (*sezekorni*). The other group occurs east of the Windward Passage, has a relatively short skull with high cranial profile, relatively short ears, and is usually dark brown (*bombifrons*).

Members of one group are most easily separated from members of the other group by differences in skull shape. The cranial height/skull length ratio is diagnostic. Thirty-six specimens of the *bombifrons* group average 37.4 (35.9–39.5) for this character whereas 159 specimens of the *sezekorni* group average 34.3 (31.9–36.9). The means of 12 samples of *sezekorni* range from 33.7 to 35.1 for this character, whereas the two samples of *bombifrons* average 37.3 and 37.5. Figure 3 shows an overlay of outlines of the two skull types modified from

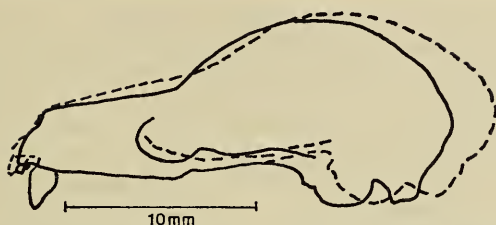


FIG. 3. Superimposed profiles of skulls of the "sezekorni type" (dashed line) and the "bombifrons type" (solid line) modified from illustrations in Hall and Kelson (1959).

illustrations in Hall and Kelson (1959). A noteworthy similarity in cranial proportions occurs between the skull profiles in this overlay and that of two subspecies of *Hylonycteris underwoodi* from Mexico and Central America illustrated in Phillips and Jones (1971). One subspecies of *H. underwoodi* is found on the Atlantic versant whereas the other occupies the Pacific versant; no zone of geographical contact has been determined.

The *bombifrons* and *sezekorni* groups too are geographically separated from each other. Thus the determination of specific or subspecific status in this case (as in the situation involving *Hylonycteris* becomes a matter of evaluation of the available morphological data. I interpret *bombifrons* and *sezekorni* to be well differentiated subspecies of *Erophylla sezekorni* as follows:

Erophylla sezekorni sezekorni (Gundlach)

Phyllonycteris sezekorni Gundlach, 1861, p. 818 (type-locality: Cuba).

Phyllonycteris planifrons Miller, 1899, p. 34.

E[rophylla]. sezekorni, Miller, 1906, p. 84.

Erophylla sezekorni syops Allen, 1917, p. 167.

Erophylla planifrons mariguanaensis Shamel, 1931, p. 252.

Distribution: Known from the Bahama Islands (including Great Abaco, New Providence, Andros, Eleuthera, Cat Island, Great Exuma, Little Exuma, Long Island, San Salvador, Crooked Island, Acklins Island, Mayaguana, and Great Inagua), from the Caicos Bank (on Providenciales, Middle Caicos, North Caicos, and East Caicos), Cuba, Isle of Pines, Grand Cayman and Cayman Brac in the Cayman Islands, and Jamaica.

Specimens examined: Great Abaco: 30(MCZ). New Providence: 58(2 AMNH, 3 AS, 6 MCZ, 47 USNM). Andros: 23(AS). Eleuthera: 13(11 AS, 2 USNM). Cat Island: 63(12 AS, 51 MCZ). Exumas: 18(Great Exuma, 5 AMNH; Little Exuma, 13 AMNH). Long Island: 12(MCZ). San Salvador: 2(AS). Crooked Island: 21(LSUMZ). Acklins Island: 1(LSUMZ). Mayaguana: 38(4 LSUMZ, 11 MCZ, 23 USNM). Caicos Islands: 39(Providenciales, 12 LSUMZ; North Caicos, 4 LSUMZ; Middle Caicos, 19 LSUMZ; East Caicos, 4 USNM). Great Inagua: 11(MCZ). Cuba: 91(Las Villas Prov., 1 MCZ; Oriente Prov., 64 AMNH, 18 MCZ, 8 USNM). Cayman Brac: 9(AS). Jamaica: 77(St. James Parish, 55 AMNH, 6 MCZ, 10 USNM; St. Elizabeth Parish, 6 AS).

Erophylla sezekorni bombifrons (Miller), new combination

Phyllonycteris bombifrons Miller, 1899, p. 36 (type-locality, near Bayamón, Puerto Rico).

Phyllonycteris santa-cristobalensis Elliot, 1905, p. 236.

Erophylla bombifrons, Miller, 1906, p. 84.

Distribution: Known from Puerto Rico and Hispaniola.

Specimens examined: Hispaniola: 48 (Haiti: Dépt. du Nord Ouest, 2 USNM; Dépt. de l'Artibonite, 46 USNM). Dominican Republic: 18(Sánchez Ramírez Prov., 2 AMNH; San Cristobal Prov., 1 USNM; La Romana Prov., 10 AS; La Altagracia Prov., 5 AS). Puerto Rico: 52(Guanica, 1 AMNH; 5.5 mi. or 8.9 km NE Utuado, 5 AS; Bayamón and vicinity, 2 MCZ, 14 USNM; 2 mi. or 3.2 km SSE El Verde, 1 AMNH; Pueblo Viejo and vicinity, 8 AMNH, 11 USNM; Vega Alta y Vega Baja, 10 MCZ).

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